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Human Perceptual Decision Making: Disentangling Task Onset and Stimulus Onset

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Abstract: The left dorsolateral prefrontal cortex (ldlPFC) has been highlighted as a key actor in human perceptual decision-making (PDM): It is theorized to support decision-formation independently of stimulus type or motor response. PDM studies however generally confound stimulus onset and task onset: when the to-be-recognized stimulus is presented, subjects know that a stimulus is shown and can set up processing resources—even when they do not know which stimulus is shown. We hypothesized that the ldlPFC might be involved in task preparation rather than decision-formation. To test this, we asked participants to report whether sequences of noisy images contained a face or a house within an experimental design that decorrelates stimulus and task onset. Decision-related processes should yield a sustained response during the task, whereas preparation-related areas should yield transient responses at its beginning. The results show that the brain activation pattern at task onset is strikingly similar to that observed in previous PDM studies. In particular, they contradict the idea that ldlPFC forms an abstract decision and suggest instead that its activation reflects preparation for the upcoming task. We further investigated the role of the fusiform face areas and parahippocampal place areas which are thought to be face and house detectors, respectively, that feed their signals to higher level decision areas. The response patterns within these areas suggest that this interpretation is unlikely and that the decisions about the presence of a face or a house in a noisy image might instead already be computed within these areas without requiring higher-order areas. *Hum Brain Mapp 35:3170–3187, 2014.* © 2013 Wiley Periodicals, Inc.

Key words: face house discrimination task; fMRI; perceptual decision-making; task preparation; left dorsolateral prefrontal cortex

INTRODUCTION

On the basis of scarce sensory evidence, people often have to decide which one of a set of alternative stimuli they perceive. Perceptual decision-making (PDM) has been studied in humans and in monkeys. In studies on humans, participants are typically required to discriminate noisy images of faces/houses and signal their responses via button presses (see Heekeren et al., 2008). Images of faces and houses lead to increased BOLD responses in distinct brain areas, the fusiform face area (FFA), and the parahippocampal place area (PPA), respectively, that are thought to be low-level feature detectors. Importantly, Heekeren et al.

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(2006) found the BOLD response in the left dorsolateral prefrontal cortex (ldlPFC) to be effector-unspecific, to be correlated with the absolute difference in BOLD response of lower level sensory areas, and to predict participants' performance (Heekeren et al., 2004). More recently, Philiastides et al. (2011) observed that rTMS applied to the ldlPFC affects participants' behavioral performance. The authors fitted a computational model (the drift diffusion model; for a review, see Ratcliff and McKoon, 2008) to the behavioral data and found that the interference effect was compatible with a decrease in the efficiency of the evidence integration.

These results are in contrast to research performed on monkeys trained to discriminate motion direction in a random dot motion task and to signal their decision with eye movements. In these studies, neural firing rates suggest that area MT acts as a motion detector and that effector-specific areas (e.g., the lateral intraparietal area) integrate this signal across time and form a decision (see Gold and Shadlen, 2007). Accordingly, although the involvement of effector-specific brain areas has also been highlighted in human PDM (e.g., Donner et al., 2009; Heekeren et al., 2004, 2006; Ho et al., 2009; Tosoni et al., 2008), it has been argued that the human brain has developed an abstract, species-specific decision-making network allowing a flexible link between deciding and acting (Heekeren et al., 2004).

The issue of what the activity in these effector-unspecific areas reflects is hotly debated (e.g., Tosoni et al., 2008). An important issue that has so far been neglected is that most, if not all, PDM studies confound task and stimulus onset, making it impossible to attribute observed brain activity to one or the other. This becomes especially relevant for structures like the dlPFC, which have also been linked to cognitive control functions that are important at task onset (e.g., Koechlin et al., 2003). For example, it has long been known that temporal uncertainty affects perceptual performance (e.g., Earle and Lowe, 1971). Knowing when a stimulus is going to appear allows us to focus our mental and attentional resources to process the upcoming stimulus more efficiently. In the case of PDM, when presenting degraded images of faces or houses, subjects know immediately that an image is being shown but they have to figure out which image is being shown. The detection of the presence of an image might therefore serve as a cue to start the more difficult task of image identification.

The present study introduced a design that dissociates the onsets of task and stimulus in a house/face discrimination task, in order to disentangle the function of areas typically labeled as decision- or feature-related. Our results suggest that the ldlPFC is involved in task preparation rather than evidence integration. We present a framework in which FFA and PPA are not simply "sensory" areas but form perceptual decisions, and in which the comparison of evidence in favor of a choice, as implied in standard decision models, is only required (and observed) if an action has to be performed. If not, participants may simultaneously form beliefs about both face and house images being present without having to compute a decision signal.

MATERIALS AND METHODS

Participants

Twenty-one healthy volunteers participated in this study (13 males aged 24.7 ± 0.688 years and eight females aged 25 ± 0.5 years (mean $\pm$ SEM)). Six subjects were excluded from the analysis either because of exceeding head movement during the scanning or because of chance-level performance in the perceptual task. The experiments were undertaken with the understanding and written consent of each subject.

Stimuli

The stimulus set comprised a total of 200 grayscale images (457×457 pixels; $10 \times 10^{\circ}$) of front-viewed faces or houses. These stimuli were used because they lead to increased BOLD responses in two distinct brain areas: the FFA (Kanwisher et al., 1997; Puce et al., 1995) and the PPA (Aguirre et al., 1998; Epstein and Kanwisher, 1998; but also see Gauthier et al., 1999; Haxby et al., 2001). The luminance histograms of the images were normalized and equalized before decomposing each image into a magnitude and a phase image using a Fast Fourier Transform (FFT). Stimulus images that were presented to the participants were obtained by recombining (inverse FFT) the average magnitude image (across the 200 magnitude images) with individual scrambled phase images. Following previous studies (e.g., Philiastides and Sajda, 2006), we used the weighted mean phase technique (WMP; Dakin et al., 2002) to generate images whose visibility could be manipulated varying the percentage of phase coherence while leaving the lower level properties of the stimuli (e.g., luminance contrast) constant. Percentage of phase coherence was adjusted for each participant individually based on performance in the training session. On average the phase coherence was 0.388 ($\pm$ 0.014) for house images and 0.283 ($\pm$ 0.005) for face images. Images were generated using MATLAB^{TM} (http://www.mathworks.fr/) and displayed via an LCD projector on a projection screen (mean luminance of 500 cd/m^2) at an approximate viewing distance of 85 cm. Stimulus presentation and response recordings were controlled using Presentation® (Version 12.2, http://www.neurobs.com).

Experimental Design

We used a continuous stimulation paradigm designed as a rapid event-related fMRI experiment: A different stimulus image (noise or signal and noise) was presented every second of the experiment. Figure 1a schematically

illustrates the temporal and spatial layout of a trial. To find out whether a decision area is independent of an effector has generally been tested by varying the effector (e.g., eye or hand) across blocks that subjects had to use to report their decisions. Opting for an alternative approach, we informed participants about which effector to use only after the stimulus offset (cf. Bennur and Gold, 2011; Rahnev et al., 2011). Each trial comprised a 6-s period of signal (Face or House), a 9-s period of observation (i.e., white fixation point meaning the stimulation is relevant for the task), and a 2-s long response frame indicating the stimulus-response mapping. This response frame was followed by a random intertrial interval (0–4 s) during which noise only images were presented. The participants' task was to attend to the stimulation when the fixation point was white in order to decide whether the stimulation presented during that period was a face or a house. Contrary to traditional experimental designs, in this setting, subjects were continuously presented with images during the entire experiment. Most of these images were not relevant for the task. Without taking into account "the observation period," subjects would consider irrelevant images and ignore relevant ones for their decision, which would lead to a decrease in performance. Additionally, participants would have to sustain their attention for long periods. Therefore, by limiting their attention to the task-relevant period, participants both minimize cognitive cost and maximize accuracy.

Participants were asked to respond as accurately as possible. No stress was put on speed since participants had no control over speed. When the response frame was displayed, they were instructed to respond by pressing a key with their left or right index fingers, depending on whether the letter corresponding to their decision (F for Face, and H for House; see Fig. 1a) was displayed on the left or right side of the screen.

Experimental conditions were defined: (1) by two signal onset to observation cue relationships, with the signal appearing either inside (0 or 3 s after observation cue onset) or outside the observation period (9 or 6 s before observation cue onset) as well as (2) by the type of stimu-

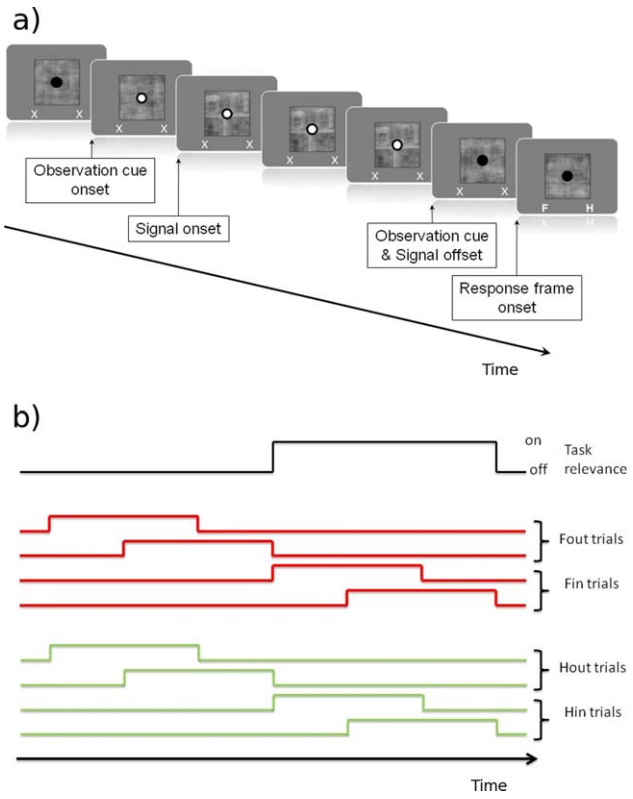

Figure 1.

Figure 1.

(**a**) Example of the temporal and spatial layout of one trial. Participants are presented with a sequence of 1 s images which contain either only noise or signal and noise images (6 s). In this example, the signal is the image of a house. The fixation point serves as an "observation cue": the period during which the observation cue is white indicates when the visual stimulation is task-relevant. The observation cue is displayed for 9 s, starting 9 s or 6 s before, or 0 s or 3 s after signal onset. This procedure allows one to temporally decorrelate the onset of the signal (face/house) from the onset of the task (integration of evidence in order to make a decision). Note also that two letters are displayed below the images and serve to instantiate SRM. When these letters are "XX" no SRM is specified. A random delay after (0–1 s) the observation cue offset the "XX" turn either into "FH" (Face→left; House→right) or "HF" (House→left; Face→right). This method temporally decorrelates the offset of the stimulus processing process from the triggering of a response. Proportions, contrasts, and signal to noise ratio in the figure have been modified for the sake of clarity. (**b**) Illustration of the experimental conditions. The upper black line indicates the time course of the observation cue, which indicates the 9 s period where the stimulation is task-relevant. Each second a new image was presented that either contained only noise or a signal (a face or a house image) embedded in noise. The next four lines in the figure illustrate the time course of the trials where faces were shown (6 s segments) with respect to the observation cue and the last four lines the equivalent time courses for house images. Thus, in different trials, face and house images were presented either inside or outside of the observation period with jittered onset times (−9, −6, 0, and 3 s). To have an explicit baseline we randomly picked 6 s segments of noise images presented during the task-relevant period when a signal was presented in the task-irrelevant period, these are called Nin in the paper. We also picked 6 s noise segments outside the observation period, when face or house images were presented inside the observation period (these segments were called Nout). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

lus (face, house, noise). The experiment consisted of three sessions: one session outside the scanner to train participants with the task and two sessions inside the scanner. Each session comprised three blocks of 36 trials (~15 min) that were separated by short breaks. In half of the trials, face or house images (equally likely) were presented during the observation period and noise only images were presented outside the observation period. In the remaining trials, face or house images were presented outside the observation period and noise only images were presented during the observation period. Participants therefore had to report if sequences of degraded images of faces, degraded images of houses, or noise only sequences contained a face or a house image. In this respect, the current procedure is similar to that used for instance by Heekeren et al. (2004) or Tosoni et al. (2008) with three differences. First, instead of using highly versus slightly degraded images of faces and houses, we used completely degraded (noise only) and highly degraded images. Second, instead of presenting single images, we decided to present sequences of images. Finally, a third difference between our design and most previous studies investigating the neural basis of PDM is that in our task subjects were informed about the stimulus-response mapping only after the decision formation period. The consequence of this last choice is that subjects are not asked to respond at the time of their decision but rather to integrate all available information and to respond when requested. This has the advantage that response preparation effects and speed-accuracy tradeoff issues are avoided. However, because we do not measure response times we cannot fit the drift diffusion model (or similar ones) to the behavioral data and compare the brain responses to the fitted parameters, as done by an increasing number of studies (e.g., Ho et al., 2009; Mulder et al., 2012; Philiastides et al., 2006).

All stimulus conditions were randomized within and across participants. The last session was followed by a 10-min localizer task in which images of noise or clearly visible faces and houses were shown to the participants.

fMRI Image Acquisition

Magnetic-resonance images were acquired using a Bruker 3T scanner equipped with a birdcage head coil at the Max-Planck-Institute of Human Cognitive and Brain Sciences (Leipzig, Germany). Visual stimuli were presented on a rear projection translucent screen positioned at the rear end of the bore of the magnet using a projector placed outside the scanning room. Participants viewed the screen via an angled mirror placed onto the head coil. Functional images were obtained with a single-shot T_2*-weighted echo-planar imaging (EPI) sequence (TE = 25 ms, TR = 2 s, flip angle = 90°). Thirty-two contiguous axial slices with a thickness of 3 mm covered the whole brain (64 × 64 matrix with a field of view (FoV) of 19.2 cm, resulting in a voxel size of 3 × 3 × 3 mm^3 with a 0.5-mm gap between slices) and were acquired in an ascending interleaved order. The main experiment and a localizer task were used to localize relevant target structures FFA and PPA were conducted in separate runs. In addition to the main experiment and the localizer task, a structural image was acquired for each participant in a separate session before this study, using a high-resolution T_1-weighted MP-RAGE sequence (TI = 650 ms; TR = 1300 ms; TE = 3.93 ms; flip angle = 10°; FoV = 256 × 240 mm^2; spatial resolution = 1 × 1 × 1.5 mm^3).

Image Processing and Analysis

The data was analyzed using MATLAB (2011b, MathWorks) and the SPM toolboxes (SPM8; Wellcome Department of Imaging Neuroscience, University College London, UK; http://www.fil.ion.ucl.ac.uk/spm/software/spm8). First images were corrected for slice timing, followed by estimating and correcting for motion and EPI deformation (realign and unwarp). Thereafter, the high-resolution anatomical image of the same subject was co-registered with the functional images, and normalization was performed using the unified segmentation approach (Ashburner and Friston, 2005). After normalization, the resulting voxel size of the functional images was interpolated to 2 × 2 × 2 mm^3. In the final step of the preprocessing, the functional images were smoothed using a Gaussian smoothing kernel of 8-mm full width at half maximum (FWHM).

The statistical evaluation was based on a least-squares estimation using the general linear model with serially correlated observations. Nonsphericity was characterized by restricted maximum likelihood (ReML) hyperparameters, which were used to whiten the data (Penny et al., 2003). In addition to the whitening, the data were temporally filtered to eliminate slow signal drifts (high-pass filter: 100 s). The design matrix was generated using the canonical hemodynamic response function without derivatives (Friston et al., 1998).

Whole-brain statistical comparisons were calculated using linear contrasts in analyses of single-subject data, and group effects were determined using a random-effects analysis at a second level (Friston et al., 1999). MRIcron (http://www.mccauslandcenter.sc.edu/mricro/mricron/) was used to create the figures. Neurological convention was used in all figures (left on the image = participants' left side).

Localizing Face and House-Specific Brain Areas

During each scan, participants viewed six alternating blocks (22 s) of faces, houses, noise images, or black screens, presented for 1 s every 2 s, interleaved with fixation periods of 6 s on average. This scan localizes brain regions in the ventral temporal cortex that are

preferentially activated by face images (FFA) or by house images (PPA).

Models of the BOLD Response for the Data Analysis

Three models were chosen to fit the BOLD responses in the present experiment. The first modeled the data assuming a 6-s-long boxcar function—convolved with a canonical hemodynamic response function—to account for the 6-s long periods where a stimulus was shown. Separate 6-s boxcar functions were used for face and house stimuli that were presented while they were task-relevant (termed "Fin" and "Hin") and for face and house stimuli that were presented while task-irrelevant (termed "Fout" and "Hout"; see Figure 1b). To have an explicit baseline, we randomly picked 6 s segments of contiguous noise images during the observation period (Nin) and outside the observation period (Nout). In addition to these six regressors, we modeled the onset of the observation period as a transient event. Other transient events included in the analysis were the onset of the stimulus-response mapping frame, the onset of the auditory feedback, and the left and right key presses. Trials where no response was emitted by the subject were not considered. All discarded trials were collapsed into an additional variable, with onset set to the offset of the previous response frame and a duration spanning the entire trial. On average there were a total of 9.438 (± 2.247 SEM) of such trials per subject.

In the second model, in addition to the regressor describe above, we subdivided the Fin, Hin, and Nin regressors depending on the response participants gave at the end of the trial (i.e., whether they reported seeing a face or a house). This model is identical to model 1 except that Fin is split into FF (face image presented and face percept reported) and FH (face image and house percept), Hin is split into HF (house image and face percept) and HH (house image and house percept), and Nin into NF (noise image and face percept) and NH (noise image and house percept).

Finally, in the third model we further split the Fin, Hin, and Nin regressors of the previous model trialwise to obtain a single regressor per trial. This model was used to evaluate if trial-by-trial fluctuations in a given regions of interest (ROI) can predict participants' perceptual responses.

Selection of Regions of Interest

Several brain regions are of particular interest in the context of PDM in a face/house discrimination task. Following previous studies, we used a separate functional localizer task to locate regions that responded preferentially either to face or to house images. To highlight face-preferring areas we computed the contrast "clearly visible faces" > "clearly visible houses" masked inclusively by clearly visible faces > "noise images" and thresholded the image at an uncorrected p value of 0.001. The equivalent contrast was computed to highlight house-preferring brain areas. Among these face- and house-preferring brain areas, we restricted our analysis to the bilateral FFA and the bilateral PPA. It should be noted at this stage that for numerous subjects only a subset of these regions could be defined using the localizer. Hence, the analysis of the BOLD responses in a given region of interest (e.g., the left FFA) only includes those subjects for which that region of interest could be defined. Therefore, the number of data points differs across ROI. The coordinates of these ROI are presented in Table I.

In addition to these ROIs, we focused our analysis on two areas that have been highlighted in the literature as being of central importance in the decision process because they appear to be independent of the motor response used to communicate the decision outcome. These two decision areas are the ldlPFC (MNI coordinates, $x = -24$, $y = 24$, $z = 36$; Heekeren et al. (2004) and the right anterior insula (raINS, MNI coordinates, $x = 41$, $y = 7$, $z = 6$; Ho et al. (2009); coordinates were converted from the reported Talaraiach into MNI system using http://imaging.mrc-cbu.cam.ac.uk/downloads/MNI2tal/tal2mni.m). The choice of these ROIs might seem arbitrary given that numerous other areas have been highlighted in PDM tasks. Our goal here is to focus on the subset of those regions that have been claimed to be action independent.

For all the ROIs, we extracted the average BOLD response out of a 3-mm radius sphere around the ROI center. These BOLD response parameters were then used for further testing, in particular to compute correlations with perceptual performance. The extraction of the contrast values (the parameters of the model fit) within these regions was performed using the rfxplot toolbox (Gläscher, 2009; revision 52, http://rfxplot.sourceforge.net/) under MATLAB. These contrast values where then analyzed using MATLAB and R (2.15.2; cran.r-project.org).

RESULTS

Behavioral Data

For each participant we computed a detection sensitivity index (d') separately for faces and houses by considering face or house images presented during the observation period as signal trials and noise images presented during the observation period as noise trials. The average (± SEM) detection sensitivity was 0.627 (± 0.139) d' for face images (d'_{Face}) and 0.852 (± 0.187) d' for house images (d'_{House}). Both d' values were different from 0 (d'_{Face} $t(15) = 4.5$, $P = 4.24\mathrm{e}{-004}$; d'_{House} $t(15) = 4.55$, $P = 3.95\mathrm{e}{-004}$). Sensitivity to face and house images did not differ across subjects ($t(15) = 0.745$; $P = 0.468$). Although each subject presented a slight bias toward reporting more often seeing a face or a house when noise

TABLE 1. MNI coordinates of the left and right FFA and PPA for each of the 16 participants included in the ROI analysis

	lFFA			rFFA			lPPA			rPPA		
Sj	*x*	*Y*	*Z*	*x*	*y*	*z*	*x*	*y*	*z*	*x*	*y*	*z*
1	−33	−49	−23	39	−28	−23	−21	−43	−14	24	−37	−14
2	−39	−55	−17	45	−46	−36	−27	−46	−11	27	−43	−11
3	−39	−49	−20				−21	−52	−17	30	−31	−17
4	−36	−55	−17	42	−34	−23	−27	−46	−8	24	−37	−17
5	−36	−40	−26	45	−37	−23	−27	−43	−11			
6							−21	−37	−17	27	−34	−17
7							−21	−40	−14	30	−31	−17
8	−42	−40	−17	42	−40	−20	−27	−52	−14	24	−37	−14
9	−36	−55	−17	45	−46	−26	−27	−61	−5	30	−55	−8
10	−36	−43	−29	36	−40	−26	−27	−49	−14	27	−34	−17
11	−45	−52	−23	39	−37	−23	−24	−46	−14	21	−37	−17
12							−24	−37	−23	27	−46	−11
13	−42	−46	−17	39	−37	−20	−30	−49	−11	30	−52	−2
14				51	−52	−20	−24	−43	−11	33	−40	−8
15	−36	−55	−17	36	−55	−20	−27	−46	−14	30	−43	−11
16	−42	−40	−23	39	−40	−23	−24	−40	−17	27	−31	−17

only images were presented, when averaging across subjects, the group was not biased (P["Face" | Noise] = 0.502 (± 0.054); z["Face" | Noise Image] = 0.014 (± 0.150); $t(15) = 0.093$; $P = 0.927$). Finally, there was a significant negative correlation between sensitivity to faces and sensitivity to houses ($r = -0.723$, $P = 0.002$), which was mediated by the bias (partial correlation between face and house d's corrected for bias: $r = 0.0497$, $P = 0.860$).

Functional Role of ROI: Predicting Perceptual Performance

If a brain area is involved in the face detection decision, then its change in BOLD response during the task-relevant period when a face stimulus is shown relative to when only noise images are shown should be proportional to the subjects' ability to detect face images[1].

In other words, across subjects, the BOLD contrast "Fin versus Nin" should correlate with d'_{Face}. Similarly, the BOLD response in the contrast "Hin versus Nin" in areas involved in house detection should correlate with participants' ability to detect houses. Note however, that attention-related areas might present a similar pattern of results: higher attentional resources might lead both to increased BOLD responsiveness (to face and house images) and to an increased perceptual performance. Decision- and attention-related areas can be differentiated by investigating whether the Fin versus Nin BOLD contrast also correlates with the house detection performance and the Hin versus Nin BOLD contrast with the face detection performance. If the perceptual ability to detect a particular type of stimulus (e.g., a face) can be predicted based on the BOLD response to any stimulus (e.g., a house) in a region of interest, then that region is likely to be involved in attention-like processes. If however, the prediction of the detection performance of one type of stimulus is specific to the BOLD response evoked by that stimulus, then that region is more likely to be involved in the decision process. A hypothetical general decision area that integrates the evidence for faces versus houses across time before leading to a decision outcome is furthermore expected to fulfill such a decisional role both for faces and for houses. Following the results reported by Heekeren et al. (2004), we expected to find such a pattern in the ldlPFC.

To study this issue, we computed partial Spearman correlations between the perceptual sensitivity to a stimulus type (d'_{Face} and d'_{House}) and an estimate of an equivalent BOLD amplitude response in diverse ROIs while controlling for perceptual sensitivity for the other stimulus type (i.e. d'_{House} and d'_{Face}) and for response bias. These

[1] *Ho et al. (2009) recently showed that, depending on the experimental setting, one might expect an overall decreased BOLD response to high evidence stimuli relative to low evidence stimuli, even though the instantaneous BOLD response increases with increasing evidence. This is because, on low evidence trials, the brain needs to integrate evidence for longer periods of time than on high evidence trials, and this increased duration might ultimately lead to an overall increased rather than decreased BOLD response for low evidence stimuli. However, in the present study, subjects were not asked to report their percept as soon as possible. Instead, their performance will be best if they integrate the evidence over the complete observation period. In this case, the integration duration is the same for both low and high evidence stimuli. Thus, we believe that the controversy raised by Ho et al. does not apply for the present experiment.*

TABLE II. Partial correlation coefficients (r) and significance levels (P) between BOLD responses in regions of interest and perceptual performance in discriminating either face images from noise only images (d'_{Face}) or houses images from noise only images (d'_{House})

	d'_{Face}∼FinNin		d'_{Face}∼HinNin		d'_{House}∼FinNin		d'_{House}∼HinNin	
ROI	r	(P)	r	(P)	r	(P)	r	(P)
lFFA	**0.707**	**0.022**	0.459	0.182	0.322	0.364	0.448	0.195
rFFA	0.463	0.178	0.301	0.398	0.187	0.606	0.304	0.393
lPPA	−0.429	0.125	0.249	0.39	−0.388	0.17	0.404	0.152
rPPA	−0.175	0.568	0.516	0.071	0.022	0.943	**0.652**	**0.016**
ldlPFC	−0.124	0.673	0.052	0.861	0.1	0.732	0.153	0.601
rains	0.109	0.711	0.292	0.312	0.268	0.354	0.453	0.104

These correlations were computed while controlling for d'_{House} and bias and d'_{Face} and bias, respectively.

equivalent BOLD contrasts were the difference in BOLD response to task-relevant face images relative to task-relevant noise images (contrast "Fin vs. Nin") or to task-relevant house images relative to task-relevant noise images (contrast "Hin vs. Nin")[2].

The partial correlation coefficients and their significance levels are presented in Table II. Significant partial correlations with d'_{Face} were observed in the left FFA (lFFA: $r = 0.707$, $P = 0.022$) but not the right FFA (rFFA: $r = 0.463$, $P = 0.178$). There was no significant correlation between d'_{Face} and the BOLD responses in the left PPA (lPPA: $r = -0.429$, $P = 0.125$) or the right PPA (rPPA: $r = -0.175$, $P = 0.568$). Similarly, we computed the partial correlation between d'_{House} and the Hin versus Nin BOLD contrast. These partial correlations were significant only for the rPPA ($r = 0.652$, $P = 0.016$); they were not significant in the lPPA ($r = 0.404$, $P = 0.152$), the lFFA ($r = 0.448$, $P = 0.195$), or the rFFA ($r = 0.304$, $P = 0.393$). To ensure that these effects in the lFFA and rPPA do not result from an attentional process, we also computed partial correlations between d'_{Face} and Hin versus Nin and between d'_{House} and Fin versus Nin. Both of these correlations failed to reach significance (d'_{Face}∼Hin vs. Nin, lFFA: $r = 0.459$, $P = 0.182$; $d'_{House} \sim$ Fin vs. Nin, rPPA $r = 0.022$, $P = 0.943$).

Next we considered the partial correlations between perceptual performance (d'_{Face} and d'_{House}) and the BOLD responses in the ldlPFC and the raINS. If these regions do indeed form the perceptual decision, then their BOLD responses should correlate with participants' perceptual performance. Contrary to this hypothesis, we did not find any correlation in the ldlPFC between the Fin versus Nin contrast and d'_{Face} ($r = -0.124$, $P = 0.673$) or between the Hin versus Nin contrast and d'_{House} ($r = 0.153$, $P = 0.601$); a general decision area would have required that both of these be significant. Similar results were observed in the raINS where no significant correlation with perceptual performance was observed (Faces: $r = 0.109$, $P = 0.711$; Houses: $r = 0.453$, $P = 0.104$).

In short, within the set of ROIs tested in this study, participants' perceptual performance in detecting faces can only be predicted using the BOLD response to faces in the left FFA and their performance in detecting houses can only be predicted using the BOLD responses to houses in the right PPA. No perceptual performance could be predicted using the BOLD response in the ldlPFC or the raINS.

Stimulus and Attention Effects

In order to further determine to what extent each ROI is involved in attentional, decisional, or sensory processes, we computed two-way repeated measures ANOVA on the BOLD responses of these regions. The two factors of these ANOVAs were "Stimulus" (faces, houses, and noise images) and "Attention" (i.e., stimuli presented during versus outside the observation period). The results of this analysis are summarized in Table III and Figure 2. Stimulus modulated the BOLD responses in the FFAs and PPAs but did not significantly affect the BOLD response in the ldlPFC or in the raINS.

To further detail the main effect of Stimulus in the FFAs and PPAs we conduced a series of paired t-tests. Left and right PPA responded more to houses than to faces (lPPA: $t(15) = 4.085$; $P < 0.001$; rPPA: $t(14) = 5.021$; $P < 0.001$) or to noise images (lPPA: $t(15) = 5.915$; $P < 0.001$; rPPA: $t(14) = 6.459$; $P < 0.001$) but did not differentiate between face and noise images (lPPA: $t(15) = 0.795$; $P = 0.439$; rPPA: $t(14) = 0.779$; $P = 0.449$). The left and right FFA, on the other hand, responded more to face than to noise images (lFFA: $t(11) = 5.633$; $P < 0.001$; rFFA: $t(11) = 4.757$; $P < 0.001$), and more to houses than to noise images (lFFA: $t(11) = 4.645$; $P < 0.001$; rFFA: $t(11) = 2.505$; $P = 0.029$). The

[2]*The use of partial correlations is justified by studies showing that the BOLD responses to an irrelevant stimulus are decreased when more resources are required for processing a relevant one (cf. Lavie, 2005). This type of effect might be critical for PDM imaging studies. Indeed, this result might contradict the claim that an area is involved in decision-making if its BOLD response increases with increasing evidence for one alternative and decreases with increasing evidence for another one (see for instance Tosoni et al., 2008).*

TABLE III. Summary results of 3 (Stimulus) × 2 (Attention) repeated measures ANOVAs

	lFFA	$n = 12$	rFFA	$n = 12$
Stimulus	$F(2,22) = 18.633$	$P < 0.001$	$F(2,22) = 8.223$	$P = 0.002$
Attention	$F(1,11) = 17.775$	$P = 0.001$	$F(1,11) = 22.067$	$P = 0.001$
Stimulus × Attention	$F(2,22) = 1.920$	$P = 0.170$	$F(2,22) = 0.359$	$P = 0.702$
	lPPA	$n = 16$	rPPA	$n = 15$
Stimulus	$F(2,30) = 20.591$	$P < 0.001$	$F(2,28) = 28.815$	$P < 0.001$
Attention	$F(1,15) = 19.288$	$P = 0.001$	$F(1,14) = 25.720$	$P < 0.001$
Stimulus × Attention	$F(2,30) = 5.561$	$P = 0.009$	$F(2,28) = 7.997$	$P = 0.002$
	ldlPFC	$n = 16$	raINS	$n = 16$
Stimulus	$F(2,30) = 0.320$	$P = 0.728$	$F(2,30) = 0.745$	$P = 0.483$
Attention	$F(1,15) = 22.606$	$P < 0.001$	$F(1,15) = 3.779$	$P = 0.071$
Stimulus × Attention	$F(2,30) = 1.011$	$P = 0.376$	$F(2,30) = 1.151$	$P = 0.330$

responses to faces were not different from the responses to houses in the rFFA ($t(11) = 1.144$; $P = 0.277$), but reached significance in the lFFA ($t(11) = 2.297$; $P = 0.042$. The ROIs in left and right FFA have been selected because these regions responded preferentially to faces in the localizer task. When face images are strongly degraded it appears that the stimulus selectivity is less apparent (for similar results, see Esterman and Yantis, 2010; Summerfield et al., 2006).

The repeated measures ANOVAs further showed that FFA and PPA were affected by task relevance or Attention because they presented an increased BOLD response during, compared with outside of, the observation period. Attention had a significant effect on the BOLD response in ldlPFC and to a lesser extend in the raINS. In these regions however, the BOLD response decreased during the task-relevant periods relative to the task-irrelevant period. It has been argued that the increased BOLD response in the ldlPFC observed in PDM tasks when comparing easy trials relative to difficult trials reflected a deactivation of the default network, rather than the consequence of decision-related process per se (cf., Tosoni et al., 2008). The present results are in agreement with that hypothesis.

The observation period puts the subject in a PDM context and requires the accumulation of stimulus-related evidence for a choice to be made. The interaction between task relevance and stimulus type (i.e., Attention × Stimulus) is therefore most interesting for our purpose given that such an interaction might suggest a role in the accumulation of evidence. This interaction was significant in the bilateral PPAs (lPPA: $F(2,30) = 5.561$, $P = 0.009$; rPPA: $F(2,28) = 7.997$, $P = 0.002$). There was no such interaction in the left or right FFA, the ldlPFC, or the raINS. Because a general decision-making area might respond to both types of signals (i.e., both images of faces and houses compared to images of noise) we ran another two-way repeated measures ANOVA on the BOLD responses in the ldlPFC and the raINS, but this time we collapsed the face and house stimulus categories into a single "signal image" category in order to gain more statistical power. In none of these two regions was the interaction Stimulus × Attention significant (ldlPFC: $F(1,15) = 1.352$, $P = 0.263$; raINS: $F(1,15) = 0.986$, $P = 0.336$).

Correlates of Perceptual Reports in the ROIs

To further characterize the role of the ROIs in PDM, we investigated whether the BOLD responses in these regions during the task-relevant period were modulated by the perceptual outcome of the trial. If FFA and PPA behave like stimulus-specific detectors, one might expect their responses to be determined by the stimulus and not by participants' perception. Alternatively, if FFA and PPA are involved in the decision process, their BOLD response should reflect the outcome of the decision (e.g., higher activity for faces perceived as faces than faces perceived as houses). For a general decision-making area, one might also expect to observe a modulation of the BOLD response with percept. Indeed, correctly perceived images (faces seen as faces and houses seen as houses) should on average produce larger BOLD responses than incorrectly perceived images (faces seen as houses and houses seen as images). For example, when subjects report seeing a face their decision is based on a larger amount of evidence when the stimulus is indeed a face than when it is not.

We extracted the average BOLD response amplitude in the ROIs for each subject and performed a 3 ("Stimulus": face, house, noise images) × 2 ("Percept": face, house) repeated measures ANOVA. The results of this analysis are summarized in Table IV and Figure 3.

In lFFA, rFFA, and lPPA a main effect of Stimulus was found, and a trend toward significance in rPPA. In all areas, the same general pattern emerged: The stimuli being represented in a given area elicited significantly the strongest BOLD response (i.e., in lFFA and rFFA the BOLD response amplitude was largest for face images, whereas in

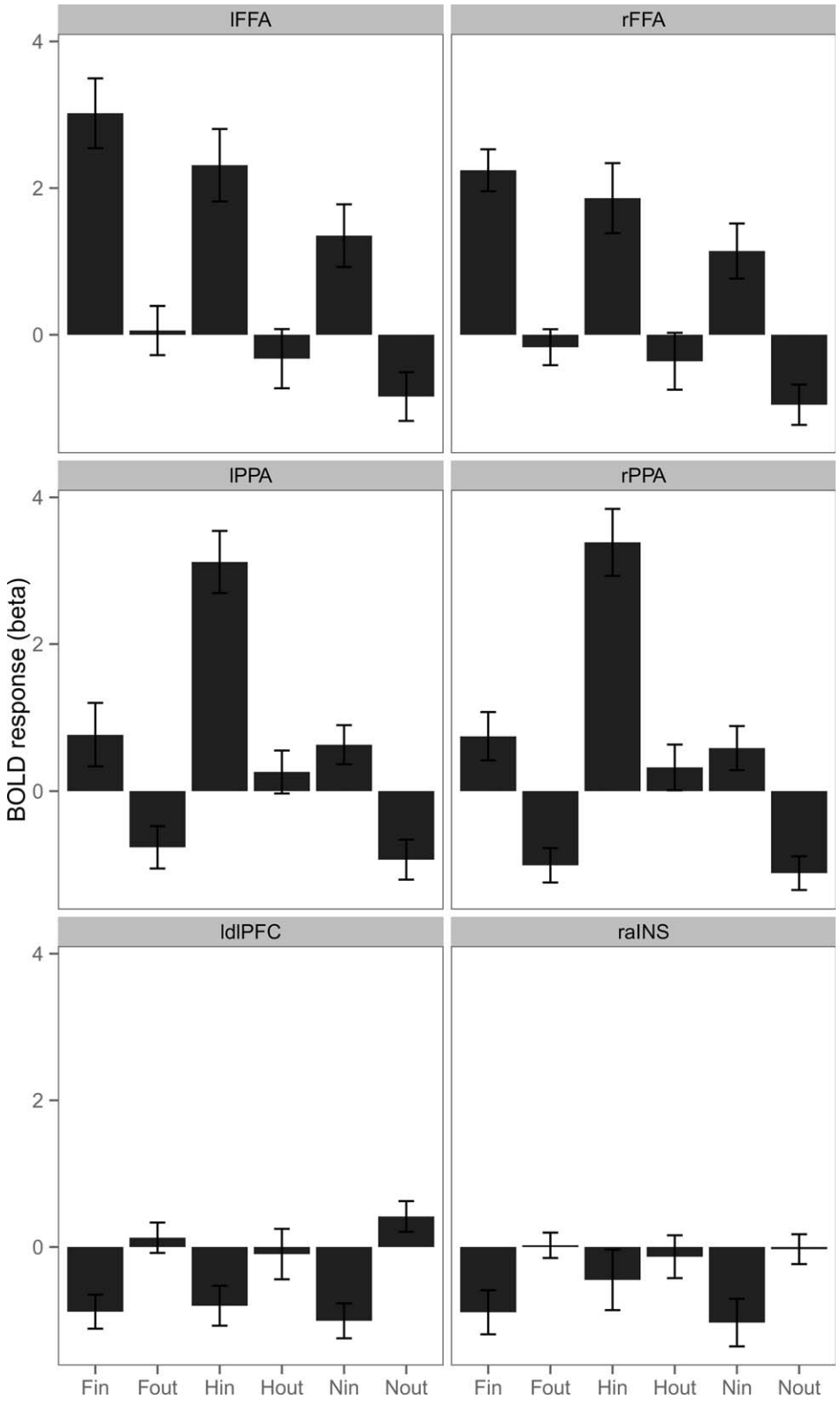

Figure 2.
(see legend on following page)

TABLE IV. Summary results of 3 (Stimulus) × 2 (Percept) repeated measures ANOVAs

	lFFA	$n = 12$	rFFA	$n = 12$
Stimulus	$F(2,22) = 5.272$	$P = 0.013$	$F(2,22) = 3.962$	$P = 0.034$
Percept	$F(1,11) = 10.427$	$P = 0.008$	$F(1,11) = 6.584$	$P = 0.026$
Stimulus × Percept	$F(2,22) = 6.819$	$P = 0.005$	$F(2,22) = 3.136$	$P = 0.063$
	lPPA	$n = 16$	rPPA	$n = 15$
Stimulus	$F(2,30) = 3.419$	$P = 0.046$	$F(2,28) = 3.215$	$P = 0.055$
Percept	$F(1,15) = 3.797$	$P = 0.070$	$F(1,14) = 11.005$	$P = 0.005$
Stimulus × Percept	$F(2,30) = 0.107$	$P = 0.899$	$F(2,28) = 0.115$	$P = 0.892$
	ldlPFC	$n = 16$	raINS	$n = 16$
Stimulus	$F(2,30) = 2.403$	$P = 0.108$	$F(2,30) = 4.929$	$P = 0.014$
Percept	$F(1,15) = 0.328$	$P = 0.575$	$F(1,15) = 0.150$	$P = 0.704$
Stimulus × Percept	$F(2,30) = 0.753$	$P = 0.479$	$F(2,30) = 1.533$	$P = 0.232$

lPPA and rPPA it was largest for house images), followed by activity elicited by the other stimulus category which however did not differ from activity elicited by noise images. The results of single *t*-tests testing for those differences are summarized in Table V. Furthermore, we observed a main effect of Percept in lFFA, rFFA, and rPPA, and a trend toward significance in lPPA. Finally, a significant interaction of Stimulus × Percept was found in the lFFA, and a trend toward significance in rFFA.

By taking into account the perceptual reports (i.e., Percept), this analysis provides less ambiguous results than the previous repeated measures ANOVA. In contrast to the previous analyses, we now observed that in lFFA and rFFA the BOLD response to face and house images differed significantly, whereas the difference between house and noise images did not. These results suggest that in these areas the stimulus-driven BOLD response to highly degraded images is masked by the additional effect of a participant's reported percept. Therefore, to establish with more certainty that a BOLD response to highly degraded images does not reflect stimulus-specific information, one must take into account participants' reports.

No significant effect was observed in the ldlPFC (Stimulus: $F(2,30) = 2.403$, $P = 0.108$); Percept: $F(1,15) = 0.328$, $P = 0.575$; Stimulus × Percept: $F(2,30) = 0.753$, $P = 0.479$). In the raINS, we observed a main effect of Stimulus ($F(2,30) = 4.929$, $P = 0.014$) with house images producing the largest BOLD response (-0.045 ± 0.215), followed by face images (-0.646 ± 0.216), and finally by noise images (-0.844 ± 0.310). Paired *t*-test showed that the BOLD responses in the raINS differed between house and noise images ($t(15) = 2.446$, $P = 0.027$) and to a lesser extend between house and face images ($t(15) = 2.921$, $P = 0.011$), but not between face and noise images ($t(15) = 0.796$, $P = 0.439$). Neither Percept nor the interaction Stimulus × Percept were significant ($F(1,15) = 0.150$, $P = 0.704$; $F(2,30) = 1.533$, $P = 0.232$).

The involvement of left and right FFA and PPA in the PDM might be addressed more directly by investigating whether their BOLD responses to noise only images predict participants' perceptual outcome. *t*-Tests revealed that on average the BOLD responses to noise images were larger in the lFFA when participants reported seeing a face (1.389 ± 0.287) than when they reported seeing a house (0.552 ± 0.308; $t(11) = 3.2113$; $P = 0.008$). A similar trend was observed in the rFFA ("face" response: 1.202 ± 0.413; "house" response: 0.502 ± 0.239) but was only marginally significant ($t(11) = 2.061$; $P = 0.064$). In the rPPA, BOLD responses to noise images were larger when subjects reported seeing a house (0.315 ± 0.417) than when they reported seeing a face (-0.201 ± 0.298) but this difference was not significant ($t(14) = -1.561$, $P = 0.141$). It should be noted that a previous study reported activations of the bilateral FFA when houses were misperceived as faces, but did not find any effect in PPA for faces misperceived as houses (Summerfield et al., 2006). It remains to be determined if this difference in behavior between the FFA and PPA reflects a qualitative difference—after all, faces are a very peculiar type of stimulus—or if instead

Figure 2.

Parameter estimates averaged across participants for the regressors (*x*-axis) used in the repeated measures ANOVAs. The first letter of the regressor name refers to the stimulus that was shown (Face, House, Noise); in and out indicates whether that stimulus was presented during the task-relevant or task-irrelevant period. Each panel represents the activity in a region of interest. Error bars are standard errors of the mean.

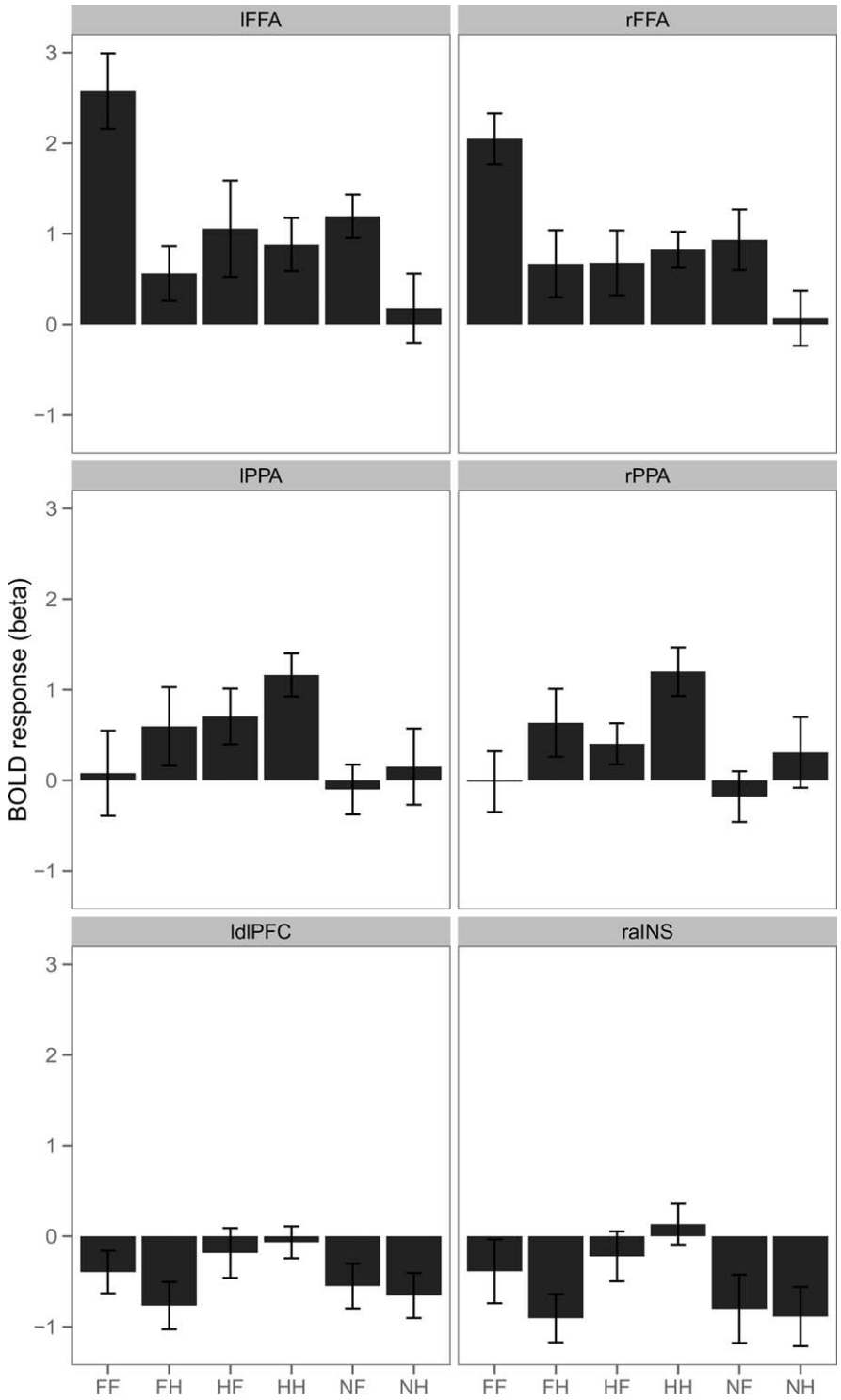

Figure 3.

Parameter estimates averaged across participants for the regressors (*x*-axis) used in the repeated measures ANOVAs. The first letter of the regressor name refers to the stimulus that was shown (Face, House, Noise), and the second letter refers to participants' reported percept. Each panel represents the activity in a region of interest. Error bars are standard errors of the mean.

TABLE V. Pairwise comparisons of the BOLD responses to faces, houses, and noise images using paired *t*-tests

Stimulus	lFFA	rFFA	lPPA	rPPA
F vs. H	$t(11) = 2.516$, $P = 0.029$	$t(11) = 2.142$, $P = 0.055$	$t(15) = 1.617$, $P = 0.127$	$t(14) = 1.905$, $P = 0.077$
F vs. N	$t(11) = 3.415$, $P = 0.006$	$t(11) = 3.472$, $P = 0.005$	$t(15) = 0.888$, $P = 0.388$	$t(14) = 0.636$, $P = 0.535$
H vs. N	$t(11) = 1.156$, $P = 0.879$	$t(11) = 0.013$, $P = 0.990$	$t(15) = 2.684$, $P = 0.017$	$t(14) = 2.132$, $P = 0.051$

both areas are qualitatively similar but misperceiving a stimulus as a house produces weaker and thus more difficult to detect brain activations than does misperceiving a stimulus as a face. This latter hypothesis, as well as the involvement of left and right FFA and right PPA in the perceptual decision beyond their commonly assumed role of sensory detectors, is further supported by the single trial analyses reported in the next section.

Trial-by-Trial Analyses

An increasing number of studies investigated the relationship between perceptual outcome and the brain activity on a trial-by-trial basis (e.g., Heekeren et al., 2004, Pessoa and Padmala, 2005, Thielscher and Pessoa, 2007). We attempted to test if such trial-by-trial correlations could be observed between the BOLD responses in our set of ROIs and participants' responses. As a first step we computed a grouped logistic regression where we regressed the probability to respond "face" (the probability of responding "house" being 1 minus this probability) as a function of the beta values of the ROI (separately for each of the six ROIs: lFFA, rFFA, lPPA, rPPA, ldlPFC, and raINS). This logistic regression model included an intercept for each subject and each condition in order to account for intersubject and intercondition differences in average BOLD responses (e.g., for some subjects the presence of a face might lead to a larger BOLD response than for others). Most importantly however, the model included a parameter that indicated to what extend trial-by-trial variations in the BOLD responses that were independent of stimulus condition affected participants' probability to report seeing a face (or a house). The results from this analysis showed that increased activity in lFFA and rFFA increases the probability that participants will report seeing a face (lFFA: coeff $= 0.039 \pm 0.010$, $P < 0.001$; rFFA: coeff $= 0.028 \pm 0.01$, $P = 0.003$). In the rPPA, we observed a negative relationship between the BOLD fluctuations and participants' tendency to respond "face" (implying an increased tendency to respond "house"; rPPA: coeff $= -0.02 \pm 0.007$, $P = 0.006$). A similar, yet only marginally significant, tendency was observed in the lPPA (coeff $= -0.012 \pm 0.007$, $P = 0.084$). No relationship was observed between perceptual outcome and the BOLD responses in the ldlPFC (coeff $= 0.006 \pm 0.008$, $P = 0.823$) or the raINS (0.006 ± 0.007, $P = 0.353$), as would be expected if these areas were general decision-making areas. Figure 4 illustrates these results graphically.

Next, we attempted to reproduce the analysis reported in Heekeren et al. (2004). These authors computed the difference in BOLD response between FFA and PPA on a trial-by-trial basis and correlated the absolute value of that difference with the BOLD response measured on those same trials in the ldlPFC. The rationale of that analysis is that, if the ldlPFC performs a readout of the evidence encoded in FFA and PPA, then the magnitude of the response in the ldlPFC should correlate with the strength of the evidence in favor of a decision option, irrespective of the option. If the difference in BOLD response between FFA and PPA is large, then the decision is easy and the ldlPFC should yield a large BOLD response. If, however, FFA and PPA have similar BOLD responses, the decision is difficult and the ldlPFC should yield a small BOLD response. In agreement with the hypothesis of a general decision-making role for the ldlPFC, Heekeren et al. reported a significant correlation between the absolute value of the BOLD response difference between FFAs and PPAs and the response of the ldlPFC.

In order to replicate this approach as closely as possible, we computed the absolute value of the differences in the trial-by-trial BOLD response to stimuli presented during the task-relevant period (i.e., Fin, Hin, Nin) between the lFFA and the rPPA for each participant (only including those subjects in the analysis for which ROIs in both areas could be localized).[3]

Next, we computed the Spearman correlation between that relative evidence signal and the BOLD responses measured on the same trials in the ldlPFC. Contrary to Heekeren et al. (2004), we did not observe a significant correlation ($r = 0.01$, $P = 0.702$). A virtually identical result was observed after performing this analysis on the raINS ($r = 0.02$, $P = 0.389$).

Pattern of Brain Activation Caused by the Task Onset

This experiment was designed to dissociate the mechanisms that are triggered by the onset of the task from those actually performing it. We hypothesized that the onset of the observation period, which signals the beginning of the

[3]*We decided to use the signals in lFFA and rPPA because these areas gave the clearest results in the preceding analyses. However, computing this correlation after averaging the left and right FFA and the left and right PPA yielded qualitatively similar results (ldlPFC: $r = 0.01$, $P = 0.579$; raINS: $r = 0.02$, $P = 0.349$; [−26, 32, 30]: $r = 0.02$, $P = 0.377$)].*

task, will essentially prompt task preparation areas whereas regions that are involved in the decision process itself, will be activated during the whole task-relevant period. We reasoned that the ldlPFC might be related, not to PDM per se, but rather to the cognitive control of the decision process. As noted in Heekeren et al. (2004), the ldlPFC has been shown to respond in "if-then" situations (cf., Koechlin et al., 2003; Petrides et al., 1993) where a cue informs participants what action to perform. In the context of a laboratory PDM task, the onset of the stimulus provides a cue that might serve to trigger these cognitive control signals (if stimulus onset, start integrating information to perform a decision). Alternatively, if the ldlPFC is indeed reading out continuously the responses of FFA and PPA to compute a decision signal, then it should not be activated by the onset of the observation period.

Figure 5a presents the pattern of brain regions showing an increased BOLD response at task onset. This figure is strikingly similar to that presented in Heekeren et al. (2004) as it shows activations in the bilateral middle frontal gyri, the supplementary eye fields, the bilateral intraparietal sulcus, as well as the posterior cingulated cortex (the bilateral insula were apparent at an uncorrected threshold of $P = 0.001$). In addition to those areas, we also observed strong activation in the occipital cortex. These results are thus in agreement with Heekeren et al.'s data in the sense that they are compatible with the frontoparietal attentional network operating—in our case it seems—on the task-relevant visual areas. Most important to our purpose, the onset of the observation period increases the activity in the left superior frontal sulcus, a region very close to the area described by Heekeren (MNI coordinates of the originally reported area: [−24 24 36]; nearest suprathreshold voxel in the present contrast: [−24 26 34], local maxima: [−26 32 30]).[4] But even when using the original coordinates, the effect of task onset was significant (small volume correction; 3 mm radius sphere centered on [−24 24 36], $P_{\text{FWE-cor}}r = 0.003$).

The results of this analysis thus suggest that the ldlPFC plays a role in PDM; not in the computation of the decision variable but rather in the organization and preparation for the upcoming task. This hypothesis fits to the fact that the onset of the observation period increases the BOLD responses in early and late visual areas, possibly to increase sensitivity. Heekeren and colleagues' finding that the activity in the ldlPFC correlates positively with participants' performance might then be explained by the fact that a better preparation is associated both with higher BOLD response in the ldlPFC and with better perceptual performance. This hypothesis could be tested directly by varying the duration of the stimulation: For short stimulus presentations, the effect of the preparation on performance should be more important than for long stimulus presentations. Furthermore, the observation that the activity in this area correlates with the absolute value of the difference in BOLD responses in Face and House areas could be interpreted as resulting from unequal top-down amplification signals rather than bottom-up integration ones.

The areas that showed an increased BOLD response at task onset in this study have been highlighted in Heekeren et al.'s study by computing two distinct contrasts. The first looked for higher BOLD amplitudes on difficult compared to easy trials and was labeled "attentional." In contrast, the second, defined regions that showed an increased BOLD response to easy compared to difficult trials and was termed "decisional." The ldlPFC area was highlighted by this second contrast. Here we observed both networks at once using a single contrast: the onset of the task. To further investigate this apparent discrepancy, we present the whole-brain activation pattern for the contrast "In versus Out" which shows brain areas that present an increased BOLD response during the task-relevant period compared to the task-irrelevant period (not only task onset as in the previous test). These results are presented in Figure 5b. This contrast yields very significant activations in the occipital cortex, the intraparietal sulcus, the medial prefrontal cortex, and the bilateral middle frontal gyri. The activations of the ldlPFC as well as the posterior cingulate cortex are absent in this contrast. The ldlPFC, that was clearly activated by task onset, remained silent during the task-relevant period (small volume correction; 3 mm radius sphere centered on [−24 24 36], no significant voxel even when we increased the sphere radius to 12 mm; same result was observed when contrasting BOLD responses to task-relevant faces and houses relative to task-relevant noise images, i.e., easy vs. difficult trials).

We believe that these prefrontal areas act as a kick-starter at task onset and drive an increase in response in the areas that remain active during the whole task-relevant period. Following this logic one could explain the discrepancy between our results and those of Heekeren et al. It might be that in their study, "salient" stimuli (easy decisions) prompted this kick-starting prefrontal regions more effectively leading to an increased boost in the attentional network. Difficult stimuli, on the other hand, might require an additional sustained activation that develops only later. Computing the difference between easy and difficult trials would then highlight only the difference in the initial kick-starting response whereas the contrast difficult > easy would highlight only the difference in the later sustained response.

DISCUSSION

In this study, participants reported whether they perceived a face or a house in a stream of noisy images containing a face, a house, or noise only. This procedure allowed us to dissociate the signal onset (face or house images) from the task onset. Our results show that the

[4] *All reported analyses have been rerun on these ROIs to assure that small differences in ROI coordinates are not determinant for our results. The results of these ROIs were virtually identical to the previous one.*

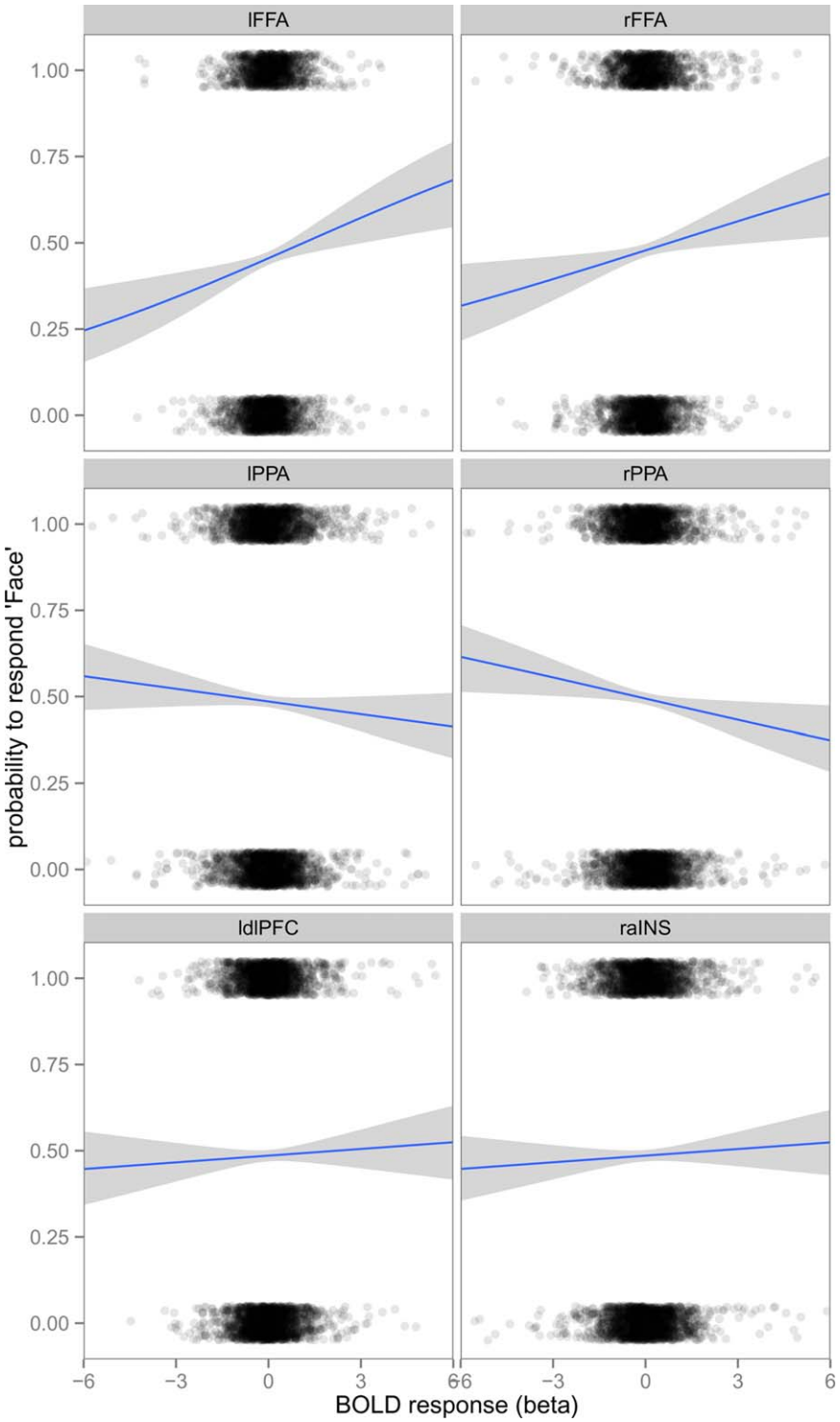
lFFA
rFFA
lPPA
rPPA
ldlPFC
raINS
probability to respond 'Face'
1.00
0.75
0.50
0.25
0.00
−6
−3
0
3
6
BOLD response (beta)

Figure 4.

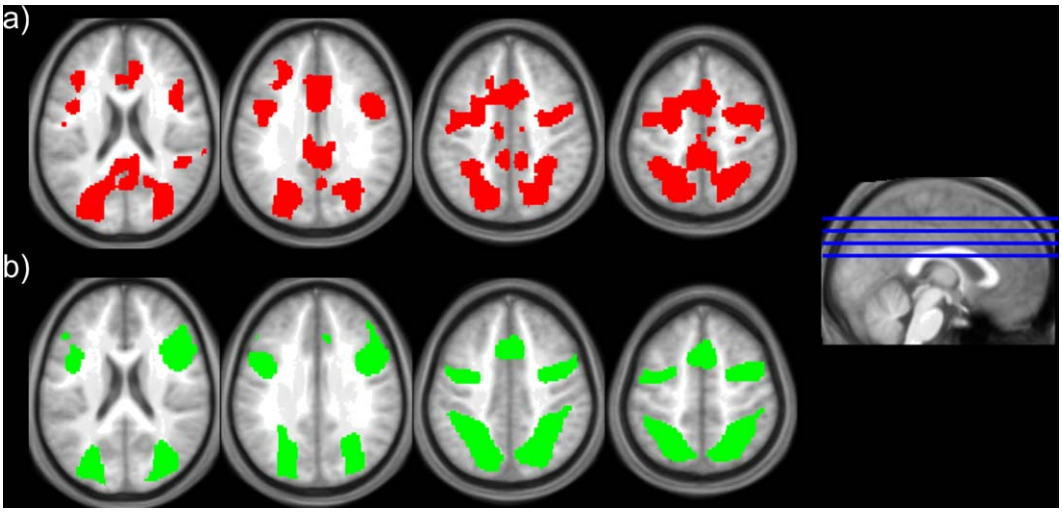

Figure 5.

Pattern of brain activation showing an increased BOLD response at the onset of the task (**a**) and during the task-relevant period compared to the task-irrelevant period (**b**) ($P < 0.05$ FWE-corrected at the cluster level). Both contrasts show widespread bilateral activations in the middle frontal gyri, the medial prefrontal cortices, the intraparietal sulci, and the occipital cortices. Additional task onset-specific activation was found in the posterior cingulate and the left dorsolateral prefrontal cortex, whereas during the task-relevant period additional activity appeared in the bilateral anterior insula. See text for details. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

task onset activates the ldlPFC as well as attentional and visual areas. However, during the task itself, ldlPFC is silent. In line with Tosoni et al. (2008) and Ho et al. (2009), the current study suggests the ldlPFC not to be a general decision-making area. We believe that the ldlPFC is involved in PDM, not as an evidence-integrator but rather as a kick-starter or chief conductor that drives activity in areas that are relevant for the task at hand. In other words, contrary to previous studies that suggested the ldlPFC played a major role in human PDM (e.g., Heekeren et al., 2004), we believe ldlPFC activation to be related to "if-then" situations (Koechlin et al., 2003; Petrides et al., 1993). In the context of PDM, the onset of the stimulus to be judged serves as a cue (if) to trigger control processes that are required to perform the task adequately (then).

In previous studies, the ldlPFC has been shown (1) to be more activated on high evidence than low evidence trials, (2) to correlate with participants' performance, (3) to have a BOLD time course in a face/house discrimination task that correlates with the absolute difference in BOLD responses between face and house selective brain regions (FFA and PPA, respectively), and (4) to led to decreased perceptual performance in a face/house discrimination task when rTMS is applied over the ldlPFC. Behavioral performance in that study was furthermore fitted with the drift diffusion model—a well-known and successful model of how humans perform binary decisions that require the

Figure 4.

Each panel represents data from one of six ROIs: the left and right FFA, the left and right PPA, the left dorsolateral prefrontal cortex (ldlPFC), and the right anterior insula (raINS). Each panel shows a logistic regression curve (solid curve) with its 95% confidence intervals (shaded area) that describe the probability that subjects respond "face" in a given trial as a function of the trial-by-trial fluctuations in the BOLD response. Each black dot represents the BOLD response observed in an individual trial (plotted at $y = 1$ or $y = 0$ depending on whether subjects reported seeing a face or a house, respectively) after subtracting the condition average BOLD response for each participant. In other words, these data points represent the trial-by-trial fluctuations in the BOLD response that are not accounted for by stimulus condition or between subject differences. Each panel contains the data from all subjects for which the ROI could be located (see Table I). Participants' responses could be predicted from the bilateral FFAs and from the right PPA (for details see text). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

accumulation of information over time. Within that model, the reduction in performance resulting from rTMS over the ldlPFC was best accounted for by assuming that it affected the drift rate parameter. This parameter describes, in essence, the efficiency of the system to compute and accumulate evidence in time. In the light of our study, these findings could be reinterpreted as follows: (1) Salient stimuli more easily prompt the kick-starting prefrontal region than nonsalient stimuli. (2) This in turn results more quickly/efficiently in high preparedness of attentional and task-relevant networks. The efficient preparation is accompanied by higher BOLD responses in the ldlPFC and results in higher BOLD responses in FFA and PPA, as well as in increased perceptual performance. (3) The activity in ldlPFC correlating with the difference in BOLD responses in FFA and PPA could result from ldlPFC modulating their activity in an unbalanced top-down fashion (e.g., due to expectation of a particular stimulus category) rather than bottom-up difference signal, indicating integration of information. (4) Applying rTMS over the ldlPFC may hamper the brains ability to prepare for the upcoming stimuli. The stimuli being less efficiently processed could manifest itself, within the drift diffusion model, as a decrease in the drift rate parameter. Our results and interpretations are in line with Philiastides et al. (2006). In their study, subjects were presented noisy images of colored faces and cars. On some trials, participants discriminated the images based on color (red vs. green, easy task), and on others based on the image category (face vs. car, difficult task). The experiment tested whether specific brain activations are determined by the stimulus, the task, or their interaction. These authors identified three EEG components. The earliest component (170 ms) was equivalent in both tasks and predicted perceptual performance in the face/car discrimination task, suggesting that it reflects stimulus-specific bottom-up processes. This early component was followed by an intermediate component (220 ms) that correlated with task difficulty and predicted the onset of the late component. The late component (300 ms) was also task-dependent and predicted perceptual performance (better than the first component). The authors suggest that, if a decision is expected to be difficult after a first evaluation of the stimulus (early component), the need of additional processes to cope with that difficulty is signaled (intermediate component), and these additional processes affect the final decision (late component). We believe that the ldlPFC might be triggered by the first evaluation signal and in turn activate the additional processes required to cope with difficult trials.

Ho et al. (2000) suggested, similar to Heekeren et al. (2004), that humans possess a general decision-making area (see also Heekeren et al., 2004). Contrary to Heekeren et al., these authors located that area, not in the left dlPFC, but in the right anterior insula (raINS). Here, we computed the same set of analyses on both of these areas. All analyses failed to support a role of these areas as decision-makers. We can only speculate as to what role the raINS plays in PDM. According to a recent review (Sterzer and Kleinschmidt, 2010), the aINS might be tracking both internal and external task demands. In Ho et al.'s study, stimulus difficulty might have predominantly affected the response in the aINS. Because subjects in our task have the additional difficulty of sustaining attention during longer periods of time, the corresponding internal task demand signal might have masked the stimulus-driven responses in raINS.

In the previous studies, the ldlPFC and the raINS were qualified as "general" because they were observed irrespective of the effector used (e.g., eye and hand movements). This does not imply however that these areas are not specific to action. In the current experiment, subjects were not informed about the stimulus-response mapping until the end of the stimulus presentation period. It would be interesting to investigate whether or not the activity of the ldlPFC and the raINS depends on the stimulus-response mapping being provided to subjects before the decision formation.

In this study, we adopted the strategy of focusing on a small, but significant set of ROIs and to perform in-depth analyses on these ROIs rather than computing a small set of analyses and considering a large number of brain regions. This strategy was motivated by the intention to formulate explicitly a set of criteria to help determine the role of an ROI in the perceptual decision process. We believe that this approach is useful because it emphasizes not only statistical significance but also conceptual consistency. We have suggested five properties that decision areas should fulfill: (c1) The BOLD response should discriminate among the relevant stimuli (i.e., it should respond differently to signal-present than to signal-absent trials; a general decision-making area might however not be able to discriminate among different signals). (c2) It should be larger during task-relevant than task-irrelevant periods. (c3) The BOLD response should be modulated by participants' percepts (a general decision-making area should present an increased response to correctly perceived stimuli relative to misperceived ones). (c4) The trial-by-trial fluctuations in the BOLD response should predict participants' responses. (c5) The BOLD responses to task-relevant face and house images should specifically predict participants' face and house detection performance, respectively (a general decision-making area should be able to predict detection performance for both types of stimuli). We applied these criteria not only to face/house-specific areas (FFA and PPA), but also to the ldlPFC and the raINS. Only two areas fulfilled all five criteria: the left FFA for faces and the right PPA for houses.

The absence in this study of decision-related activations in the ldlPFC and in the raINS was unexpected and it might be argued that this failure would not have occurred had these regions been localized for each participant. We believe that, at least with respect to the ldlPFC, this hypothesis is not very likely for at least two reasons. First, the localization of the ldlPFC varies only slightly across

decision-making studies and in a recent experiment (Philiastides et al., 2011), rTMS were applied to this region without using prior localizer and, nevertheless, successfully affected the behavioral outcome. Second, we computed whole-brain analysis that contrasted high evidence stimuli to low evidence stimuli (Fin+Hin>Nin) and lowered the thresholds considerably to look for activations that might have been missed by our ROI: no such activations were observed. However, these doubts are nevertheless legitimate, and we regret not having anticipated this issue while data collection was still possible.

It appears from both ours and other studies that FFA and PPA cannot be considered as simple feature detectors. Summerfield et al. (2006) have reported FFA activations in response to images of houses that were misperceived as faces. Furthermore, Egner et al. (2010) tested whether FFA behaves like a feature detector by measuring BOLD responses to (clearly visible) images of faces in FFA after a cue induced varying degrees of expectation that a face was to be shown. If FFA was a face detector, its BOLD response should not be affected by expectation: Their results clearly reject the feature detection model. The FFA and PPA have also been extensively investigated in the field of consciousness research. Using a dichoptic color fusion technique whereby perception is kept constant (subjects perceive a uniform yellow field although alternating images of faces and houses are shown), Moutoussis and Zeki (2002) observed that the FFA and PPA showed preferential activation for images of faces and houses, respectively, suggesting that these areas behave like stimulus-specific detectors. The response in these areas was present but nevertheless reduced compared to the situation where participants actually perceived a face or a house. An alternative approach used binocular rivalry, where the presentation of an image of a face to one eye and the image of a house to the other eye produces the alternating perception of a face and a house, despite the retinal images being constant. Using fMRI it was observed that activity in the FFA and PPA correlated with participants' reported percepts: FFA was activated when a face was perceived, and the PPA was activated when a house was perceived (Tong et al., 1998). Activity in these areas therefore reflected participants' perception rather then the physical stimulus. Although the roles played by the FFA and PPA are not yet clear, it appears that describing them as simple detectors is at best an oversimplification.

It is important to note that whereas it is in principle possible to simultaneously see a face and a house (as when superimposing transparent images), there are stimuli for which alternative perceptions are mutually exclusive (e.g., the Necker cube). It is therefore not obvious that results obtained on the random dot motion task should generalize to face/house discrimination tasks. In the former case, it is assumed that areas like LIP integrate the sensory signals represented in MT to form a decision signal. In the latter case, as outlines above, we believe that perceptual decisions might be formed simultaneously in FFA and PPA for face and house percepts, respectively (cf. "microconsciousness"; Zeki, 2008).

In this study, we did not investigate motor response related activity. We isolated activity related to the PDM from motor activity by informing subjects about the stimulus-response mapping (SRM) only at the end of the trial (see also Bennur and Gold, 2011; Rahnev et al., 2011). However, as noted already by Bennur and Gold (2011), this procedure does not guarantee that any motor response is prepared: subjects might, for example, prepare a verbal response and switch to the SRM that is presented at the end of the trial. It is difficult to find a paradigm that by design excludes such effects. An interesting methodological alternative might be to use motor preparation signals to track the decision processes that drive them (e.g., Donner et al., 2009). The results of Donner et al. are in line with the continuous flow model of human information processing (see Coles et al., 1985). On this account, in situations (unlike in the present study) where the SRM is made known to subjects before the stimulus presentation, decision areas feed motor execution process continuously with information while they are processing the stimulation. Using fMRI, Tosoni et al. (2008) selected regions in the parietal cortex based on the fact that they were specifically activated by hand or eye movements. Next, they asked human subjects to discriminate noisy images of faces and houses. Face percepts were to be reported by making an eye movement, and house percepts by making a pointing movement. The effector-specific regions in the parietal cortex increased their activity when the evidence favoring that effector increased (e.g., higher face evidence was associated with higher activity in the eye movement-specific parietal regions). No general decision-making area was observed.

These results are compatible with ours if one assumes that the decisions about the presence or absence of faces and houses are formed in FFA and PPA, respectively (as evidenced by our study), and that they continuously feed their signals to "dumb" effector-specific areas when the SRM are known (as shown in Tosoni et al., 2008). The alternative hypothesis according to which FFA and PPA are dumb feature detectors and that effector-specific regions form the decision signal by integrating the output of such detectors across time seems more unlikely.

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